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Barriers to seed and seedling survival of once-common Hawaiian palms: the role of invasive rats and ungulates

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Abstract. Mammalian herbivores can limit plant recruitment and affect forest composition. Loulu palms (*Pritchardia* spp.) once dominated many lowland ecosystems in Hawai'i, and non-native rats (*Rattus* spp.), ungulates (e.g. pigs *Sus scrofa*, goats *Capra hircus*) and humans have been proposed as major causes of their decline. In lowland wet forest, we experimentally determined the vulnerability of seeds and seedlings of two species of *Pritchardia*, *P. maideniana* and *P. hillebrandii*, by measuring their removal by introduced vertebrates; we also used motion-sensing cameras to identify the animals responsible for *Pritchardia* removal. We assessed potential seed dispersal of *P. maideniana* by spool-and-line tracking, and conducted captive-feeding trials with *R. rattus* and seeds and seedlings of both *Pritchardia* species. Seed removal from the forest floor occurred rapidly for both species: >50 % of *Pritchardia* seeds were removed from the vertebrate-accessible stations within 6 days and >80 % were removed within 22 days. Although rats and pigs were both common to the study area, motion-sensing cameras detected only rats (probably *R. rattus*) removing *Pritchardia* seeds from the forest floor. Captive-feeding trials and spool-and-line tracking revealed that vertebrate seed dispersal is rare; rats moved seeds up to 8 m upon collection and subsequently destroyed them (100 % mortality in 24–48 h in captivity). Surprisingly, seedlings did not suffer vertebrate damage in field trials, and although rats damaged seedlings in captivity, they rarely consumed them. Our findings are consistent with the hypothesis generated from palaeoecological studies, indicating that introduced rats may have assisted in the demise of native insular palm forests. These findings also imply that the seed stage of species in this Pacific genus is particularly vulnerable to rats; therefore, future conservation efforts involving *Pritchardia* should prioritize the reduction of rat predation on the plant recruitment stages preceding seedling establishment.

Keywords: Island biology; *Rattus exulans*; *Rattus rattus*; seed dispersal; seed predation; seedling herbivory; *Sus scrofa*; tropical palm forest.

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Introduction

Alterations to island ecosystems resulting from introduced mammals are well documented across the world (Vitousek *et al*. 1997; Courchamp *et al*. 2003; Blackburn *et al*. 2004; Traveset and Richardson 2006). Aside from humans, perhaps the most ubiquitous introduced (non-native) mammals negatively affecting island flora and fauna are ungulates and rats; these non-native vertebrates are invasive because they spread rapidly and cause ecological or economic harm (Lockwood *et al*. 2007). Indeed ungulates and rats are commonly implicated in local extinctions and species reductions at multiple trophic levels, and they disrupt ecological processes (Singer 1981; Hone 1995; Vitousek *et al*. 1997; Courchamp *et al*. 2003; Towns *et al*. 2006). A well-accepted reason for these invasive vertebrates causing such ecosystem-changing effects in insular environments stems from the absence of similar native vertebrate species, and therefore includes the novel behaviours that are characteristic of such invasive herbivores (e.g. chewing, rooting, trampling).

The seed and seedling stages of the plant life cycle are typically more vulnerable than adults to the negative effects of rats and many ungulates. Seed predation by native and non-native mammals can limit plant recruitment and ultimately affect forest composition and structure (DeSteven and Putz 1984; Cabin *et al*. 2000; Campbell and Atkinson 2002). Alternatively, consumption of seeds may sometimes result in dispersal of native and non-native plant species (Abe 2007; Shiels and Drake 2011; O'Connor and Kelly 2012). Until relatively recently, the role of non-native rats (*Rattus* spp.) as a primary cause of insular forest and ecosystem change received little attention, perhaps because changes in tree communities typically occur over greater time scales than human life spans, written documentation was often uncommon during the years following rat introductions to islands, palaeoecological baselines were not widely documented and because rats are generally nocturnal and thus their links to causing change are not always obvious (Shiels *et al*. 2014).

Palaeoecological studies have documented the decline of many Pacific Island palm (Arecaceae) species following the arrival of humans (Prebble and Dowe 2008). At least two studies provide evidence supporting non-native rats as partially responsible for island-wide vegetation changes (Athens *et al*. 2002; Hunt 2007). In both cases, the plant life-form suffering decline was a palm—the Jubaea palm (now extinct, but related to the extant *Jubaea chilensis* of South America) in Rapa Nui (Easter Island; Hunt 2007) and the Loulu palm (*Pritchardia* spp.) in Hawai'i (Athens *et al*. 2002; Athens 2009). Of the 25 species of Hawaiian *Pritchardia* currently recognized by Wagner *et al*. (1999), most survive only in small numbers and few locations, and at least eight are endangered (Chapin *et al*. 2004). Palms, which typically have large seeds relative to other co-occurring species, are well-known food items in rat diets (Pérez *et al*. 2008, Auld *et al*. 2010). Humans and rats colonized many Pacific islands simultaneously, because *R. exulans* was either a stowaway or was intentionally carried on early Polynesian watercraft. Most Pacific islands, like Hawai'i and Rapa Nui, lacked native ground mammals. Most *Jubaea* fruit endocarps recovered from archaeological sites on Rapa Nui bear rat incisor marks (Hunt 2007), and radio-carbon dates on these specimens match the time period of island-wide *Jubaea* deforestation. A few hundred years after humans and rats colonized Hawai'i, there was a major shift in vegetation from *Pritchardia*-dominated lowland forests to a grass- and shrub-dominated ecosystem (Athens *et al*. 2002). By examining palaeoecological evidence (e.g. pollen records, rat bones, radio-carbon dating charcoal) in the most arid region of Oahu, Athens *et al*. (2002) described a chronology of *Pritchardia* forest decline that was coincidental with little human impact or settlement but an abundant local rat population. Their findings support the hypothesis that rats were partially responsible for the large-scale deforestation of *Pritchardia*-dominated dry landscapes in Hawai'i. The most likely mechanism for large-scale rat-induced deforestation of native palms in both Rapa Nui and Hawai'i is through rat predation of seeds and perhaps seedlings (Hunt 2007; Athens 2009).

Invasive pigs (*Sus scrofa*) and goats (*Capra hircus*) have also been linked to native plant damage and mortality in insular ecosystems (Coblentz 1978; Barrios-Garcia and Ballari 2012). Whereas goats were introduced to Hawai'i following European contact in 1778, Polynesians introduced pigs (probably descendants from the Asiatic form of *S. scrofa*) upon their arrival ~700 years ago. Through rooting, trampling and herbivory, pigs reduce native plant abundance and cover in many wet forests in Hawai'i (Drake and Pratt 2001; Cole *et al*. 2012; Murphy *et al*. 2014). In drier habitats in Hawai'i, goats threaten native plants, particularly seedlings, by browsing and trampling (Scowcroft and Hobdy 1987). Although no formal studies have investigated ungulate herbivory on native *Pritchardia*, a combination of fencing to exclude ungulates (particularly goats) and rodenticide bait application to control rats resulted in elevated seedling recruitment and a 9-fold increase in juvenile abundance in the understory after 7 years in one of the largest remaining stands of the endangered *Pritchardia kaalae* on O'ahu (Mosher *et al*. 2007). Therefore, goats, pigs and rats may play an important role in suppression of *Pritchardia* regeneration and ultimately the survival of these now uncommon palm stands (Chapin *et al*. 2004).

In this study, we addressed the following three questions. (i) Are *Pritchardia* seeds and seedlings vulnerable to predation by vertebrates in a wet forest in Hawai'i? (ii) Are there particular animals responsible for the negative impacts on these once-common palms? (iii) Are *Pritchardia* seeds likely to be dispersed by non-native rats? In contemporary conditions, this study tests the hypothesis that invasive rats can limit *Pritchardia* plant recruitment; study outcomes will also provide corroborative evidence for the palaeoecological inferences implicating rats in the demise of the Hawaiian *Pritchardia* forests.

Methods

Study site

This study took place in a tropical wet forest on the eastern border of Lyon Arboretum on the island of O'ahu, Hawai'i (21°17′N 157°50′W). The Arboretum is a 50 ha reserve at the back of Mānoa Valley, and it is bounded on three sides by steep, forested slopes. During the study period (2005–06), the average temperature at the Arboretum was ∼21–24 °C and rainfall was 3694 mm year^{-1} (R. Baker, unpubl. data). Elevation ranged from ∼210 to 230 m above sea level (a.s.l.). Most of the Arboretum is forested with a high dominance of non-native plants; many of the plant species were planted and later spread and established to other parts of the valley and island. Vegetation ground cover to 50 cm height across the study area averages 34 % (range: 0–84 %; based on measurements in 24 1 m^2 plots). The canopy is continuous, reaching heights of >25 m, with albizia (*Falcataria moluccana*; Fabaceae), blue marble (*Elaeocarpus angustifolius*; Elaeocarpaceae) and figs (*Ficus* spp.; Moraceae) common. Non-native palms (e.g. *Livistona* spp., *Veitchia* spp.; Arecaceae) are abundant in both the canopy and the understory, but there are few (<10 indiv.) *Pritchardia* spp. in the Arboretum.

As elsewhere in Hawai'i, non-native vertebrates are common in the Arboretum's forests, and these vertebrates include at least three species of non-native rodents (*R. rattus*, *R. exulans*, *Mus musculus*; M. Wong, unpubl. data), mongoose (*Herpestes auropunctatus*), pig (*S. scrofa*) and many birds (e.g. passerines, doves, parrots). Feral cats and dogs have also been observed in the area, and pig hunting is common in the uninhabited parts of Mānoa Valley, including occasionally within the Arboretum. The only native vertebrates in and around the Arboretum include O'ahu 'amakihi (*Hemignathus flavus*) and 'apapane (*Himatione sanguinea*), which are both small forest birds (10–20 g) that are unlikely to be capable of dispersing native *Pritchardia* seeds. Carlquist (1974) noted that the seeds and fruits of the Hawaiian *Pritchardia* are much larger than those of the southwest Pacific. Furthermore, there are no obvious contemporary native animal dispersers of Hawaiian *Pritchardia* seeds, yet Culliney *et al.* (2012) demonstrated that species such as the endangered crow (*Corvus hawaiiensis*), or perhaps its extinct congeners, could have been important dispersers prehistorically.

Within the 50 ha site, the focal area of the study included a 6-ha section of closed-canopy forest bordering State forestry land and located on the east side of the stream flowing from Aihualama Falls. This forest section was chosen because of the infrequency of visitation by people (mainly visitors to the Arboretum); however, the Arboretum staff visits the area ∼3–4 times per year to remove weeds around some of the planted ornamentals.

Post-dispersal seed removal

Two *Pritchardia* species (*P. hillebrandii* and *P. maideniana*) were used in field experiments to assess fruit and seed attractiveness and removal from the forest floor by vertebrates. *Pritchardia maideniana* (endangered; syn. *P. affinis*; endemic to Hawai'i Island) has ripe fruits that are approximately twice the size (fresh mass: 6.15 ± 0.32 g; length × width: 2.48 ± 0.04 × 2.15 ± 0.04 cm; $N = 15$) of those of *P. hillebrandii* (species of conservation concern; fresh mass: 2.50 ± 0.09 g; length × width: 1.72 ± 0.02 × 1.69 ± 0.03 cm; $N = 20$; endemic to Moloka'i Island). For each species, 24 stations were established along three separate transects (48 stations and 6 transects in total). Owing to the availability of ripe fruit and treatment material (e.g. cameras and vertebrate exclusion material; see below), the two experiments occurred separately. Trials for *P. hillebrandii* began on 1 November 2005, and trials for *P. maideniana* began on 5 April 2006; each trial lasted 42 days. For each species, stations were at least 25 m apart on the forest floor, and one of the three treatment levels was randomly assigned ($n = 8$ for each treatment level): (i) no-vertebrate-access (NVA), which consisted of a wire metal-mesh (0.5 cm aperture) rectangular box (20 × 15 × 5 cm; length × width × height) that excluded all vertebrates (e.g. rodents, pigs, birds) and served as the control for subsequent treatments, (ii) small-vertebrate-access (SVA), which was composed of metal mesh (1 cm aperture) that enclosed a 20 × 20 × 20 cm (length × width × height) area but had an 8 × 8 cm opening on each side that allowed small vertebrates (e.g. rodents, possibly mongoose) to access the interior but excluded larger vertebrates and (iii) open forest floor (OPEN), where all animals were able to freely access the station. Each exclosure was held in place using 8-cm-long turf staples, and the open sites were marked with the same turf staples so that fruits could be easily relocated by the investigators. Although ground cover vegetation was variable, each microsite

where fruit was placed was similar in soil type, soil depth and percentage rockiness.

Approximately 100 ripe fruits of *P. maideniana* and 300 ripe fruits of *P. hillebrandii* were collected from trees at the University of Hawai'i at Mānoa (UH) campus (~4 km from the study site). Two conspecific fruits were placed at each station (i.e. 48 fruits in total for each species). Fruit (and hereafter seed) removal was monitored periodically (1, 2, 6, 8, 13, 20, 22, 34, 42 days) over the course of the 6-week study for each species, and removed seeds were not replaced with fresh seeds. Additionally, two motion-sensing cameras (Bushnell brand) were installed on a randomly chosen OPEN and SVA station for each trial.

Potential seed dispersal

In an attempt to determine the fate of the *Pritchardia* seeds, 10 *P. maideniana* fruits from the same batch originally collected for the trials described above were set out singly on the forest floor between 20 November and 5 December 2005. Each fruit was attached to a spool of coloured thread by passing the thread through the pericarp and knotting the end before suspending the spool on a turf staple such that it would spin freely when pulled. After 48 h, the fruit was revisited, the thread was followed from its origin and the distance to the end of the thread was measured to estimate the distance that the fruit and seed was moved by the animal. *Pritchardia hillebrandii* was not assessed for potential seed dispersal.

Seedling predation in the field

In order to test the vulnerability of *Pritchardia* seedlings to vertebrates, we grew seedlings of *P. maideniana* and *P. hillebrandii* from fresh fruits/seeds collected from the same trees used in the seed removal trials. Ripe fruits were buried just below the soil surface in a potting soil: sand mixture (3 : 1 ratio) in pots placed outdoors in partial shade and watered approximately every second day. For *P. maideniana*, 84.6 % of seeds germinated ($N = 22$), and for *P. hillebrandii* 66.7 % of seeds germinated ($N = 24$); the average time to germination (number of days to first emergence of the shoot) was 94.4 ± 5.2 days for *P. maideniana* (*P. hillebrandii* not measured).

On 2 March 2006, 24 seedlings of *P. maideniana* (mean ± SE height: 17.9 ± 0.6 cm), and on 18 September 2006, 24 seedlings of *P. hillebrandii* (mean ± SE height: 16.7 ± 0.4 cm), were planted near to, and in the same three treatment levels as, the seed removal trials. The dimensions of the NVA were 20 × 20 × 20 cm (length × width × height) and the metal mesh (1 cm aperture) that surrounded the seedling lacked a floor. Seedlings were randomly assigned treatment levels (NVA, SVA, OPEN; $n = 8$ for each) along transects and each station was at least 25 m from an adjacent seedling station. Seedlings were ~4–5 months old and had at least two leaves when outplanted. Seedlings were monitored at least weekly for 3 months, then monthly for an additional 3 months, to assess seedling damage and mortality. Three motion-sensing cameras were randomly positioned at OPEN and SVA stations to monitor vertebrate visitation and seedling consumption during the first 3 months of the trials. All seedlings of both species were measured for height (base of the shoot to the furthest green structure, which was usually the tip of the longest leaf) at the time of outplanting, and 6 months after outplanting.

Seed and seedling predation trials with captive wild rats

We conducted a series of captive-feeding trials by offering either fresh fruits (and seeds) or seedlings of *P. maideniana* and *P. hillebrandii* to *R. rattus* individuals, using the methods described in Shiels and Drake (2011). For each trial, at least seven adult rats (*R. rattus*) were captured from wild populations in mesic forest sites within the Wai'anae Mountains, O'ahu, transported to a rodent housing facility at Lyon Arboretum, and held in 38 × 22 × 18 cm metal-mesh cages (one rat per cage). Rats were allowed to acclimate for at least 1 week before beginning feeding trials and for at least 5 days between trials, during which time the rats were fed a diet of mixed seeds (e.g. corn, sunflower, wheat, barley, oats, sorghum) and fruit wedges (tangerine). Rats were checked daily in order to ensure ample food and fresh water.

Two feeding trials took place to assess seed predation, one for *P. hillebrandii* and one for *P. maideniana*. Each of the seven rats was offered three ripe fruits of *P. hillebrandii* (13 July 2007) and 18 days later two ripe fruits of *P. maideniana*. A dish of fresh water was always present in each rat's cage. Visual inspection occurred after 24 and 48 h to estimate the percentage of fruit and seed mass remaining. Seeds were classified as destroyed if the embryo was eaten or >50 % of the seed mass had been eaten (Shiels and Drake 2011).

Seedling damage by rats was assessed in two trials where 10 rats were offered a single seedling, each ~10–25 cm tall with one to two leaves, of either *P. hillebrandii* or *P. maideniana*. On each trial date (21 June 2008 and 11 July 2008), five rats received *P. maideniana* seedlings and five rats received *P. hillebrandii* seedlings such that no rat was exposed to the same species more than once. Each seedling, offered in a 10-cm-diameter and 10-cm-tall pot of soil, was placed in each rat's cage with a dish of water but no other food. After 24 h, each seedling was inspected and quantified (by visual estimate) for the amount of

aboveground seedling mass consumed, and damaged, by each rat.

Statistical analysis

At the end of the 42-day post-dispersal seed removal trials, and at the end of the 6-month seedling predation trials in the field, Kruskall–Wallis tests (assumptions of analysis of variance were not met) were administered for each species to compare the proportion of seed removal (or seedling mortality) as a function of our vertebrate treatment (all vertebrates excluded, access to small vertebrates, and access to all animals). When the vertebrate treatment was significant, we performed multiple comparison tests to determine differences among means. For captive-feeding trials, the damage to seedlings was compared between plant species using Student's *t*-test upon meeting assumptions of parametric testing. Statistical analyses were performed using *R* version 2.12.0.

Results

Post-dispersal seed removal

Vertebrates readily removed *Pritchardia* seeds positioned on the forest floor. For *P. maideniana* and *P. hillebrandii*, all seeds remained in the NVA (control) (Fig. 1), which resulted in significant differences when the three treatment levels were compared for *P. hillebrandii* (d.f. = 2; $\chi^2 = 16.1$; $P < 0.001$; Fig. 1A) and *P. maideniana* (d.f. = 2; $\chi^2 = 16.9$; $P < 0.001$; Fig. 1B). Identical proportions of available seed (SVA and OPEN) were removed (87.5 %) at the end of the 6-week (42-day) study for *P. hillebrandii* (d.f. = 1; $W = 32$; $P > 0.999$; Fig. 1A), and the proportion of seed remaining after the same duration for *P. maideniana* was not significantly different between SVA and OPEN (d.f. = 1; $W = 20$; $P = 0.076$; Fig. 1B). The only animals photographed by the motion-sensing cameras were rats (probably *R. rattus*; Fig. 2), and the images of rats visiting seed of both species coincided with the removal of seed from the forest floor. Seed removal by vertebrates occurred rapidly, as indicated by at least 50 % seed removal within 6 days in stations accessible to vertebrates (SVA and OPEN) (Fig. 3). The rapid removal during the first week was followed by a slower, more gradual, removal over the next 2 weeks, whereas the final 3 weeks had a total of only two seeds removed for each species (Fig. 3).

Potential seed dispersal

Five of the 10 *P. maideniana* fruits that were attached to spools of threads were moved a distance of >10 cm, two fruits were moved only 15–20 cm and three fruits were moved >3 m. Fruits attached to the spools of thread were never recovered, and both moved and unmoved fruits appeared to have the thread chewed off where it

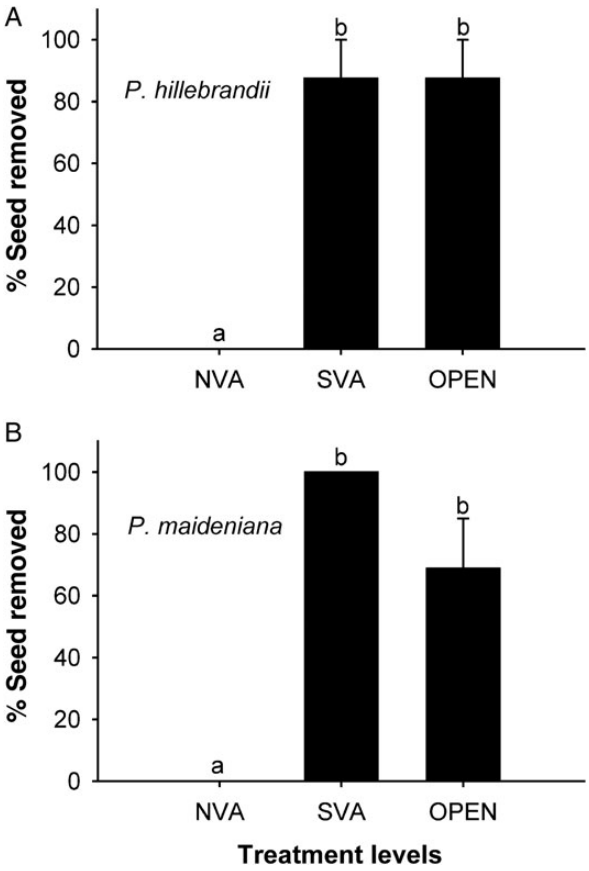

Figure 1. Mean (±SE) seed removal of (A) *P. hillebrandii* and (B) *P. maideniana* from the forest floor after 42 days of study in Hawai'i. Different lowercase letters represent significant ($P < 0.05$) differences among treatment levels ($n = 8$ for each treatment level) within each species. NVA, no-vertebrate-access; SVA, small-vertebrate-access and OPEN, access for all animals.

Figure 2. Photograph taken by a motion-sensing camera depicting *R. rattus* removing fruit (and seed) of *P. hillebrandii* from an OPEN station, in Hawai'i wet forest (Lyon Arboretum). One characteristic that identifies the photographed rat as *R. rattus* is the very long tail (longer than the body; see Shiels *et al.* 2014).

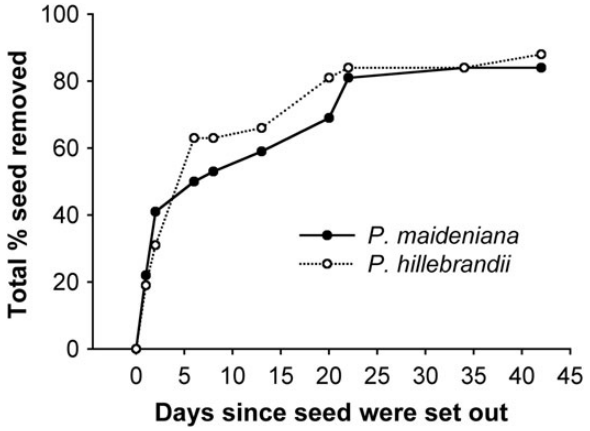

Figure 3. Percent *P. maideniana* and *P. hillebrandii* seed removal from the forest floor over 42 days of study in Hawai'i ($N = 32$ seeds/species). Seeds included here were those available to vertebrates (i.e. those in the SVA and OPEN and not in the NVA).

is attached to the fruit, or more commonly the fruit was pulled off the thread, leaving only the knot remaining on the string. Therefore, the measured fruit movement distances were likely underestimates of the true distances moved. The fruits that were not moved >10 cm had the threads caught on vegetation, or the spool was not functioning properly (not freely spinning when pulled) when revisited. The maximum distance that fruit was moved in a single trial was 8.05 m, whereas the average distance moved for those moved >10 cm was 3.28 ± 1.48 m. In all cases where fruit was moved, the thread revealed the movement was either lateral or uphill in reference to the sloping topography, and never up into trees. In one case the fruit was moved 3.4 m up a 30° slope. In all cases where fruit was moved >10 cm, the thread was taut, low to the ground and often under vegetation that was <30 cm high; these findings are consistent with the removal by a small (<30 cm tall) animal.

Seedling predation in the field

In the field, there was no evidence of seedling predation or herbivory damage to either *Pritchardia* species during the 6-month study. Seedling survival was high for *P. maideniana* (95.8 %) and *P. hillebrandii* (87.5 %). The only *P. maideniana* seedling that died was in the NVA, and there was no significant difference among treatment levels (d.f. = 2; $\chi^2 = 2.0$; $P = 0.368$). Similarly for *P. hillebrandii*, one of the three seedlings that died was in NVA while the other two were in the OPEN; there was no significant difference among treatment levels (d.f. = 2; $\chi^2 = 2.2$; $P = 0.335$). All dead *Pritchardia* seedlings were upright in the spot where they had been planted, fully intact (no evidence of herbivory) and dessicated. Several times during the experiments pig disturbance was evident within the study site, as indicated by expanses of overturned soil, overturned exclosures and pig tracks found in close proximity (sometimes <30 cm) to the seedlings. Motion-sensing cameras also photographed pigs and rats in the vicinity and passing by the seedlings, but never closer than 30 cm from the seedlings. Both species of *Pritchardia* exhibited growth in the field; *P. maideniana* grew 8.4 ± 1.2 cm and *P. hillebrandii* grew 5.1 ± 0.6 cm in a 6-month period. Similar to field growth, *P. maideniana* grew 9.3 ± 0.8 cm and *P. hillebrandii* grew 4.2 ± 0.6 cm in pots on outdoor benchtops at UH during the equivalent 6-month period.

Seed and seedling predation trials with captive wild rats

Captive wild *R. rattus* readily consumed most seed tissue of both *Pritchardia* species, and such active feeding on the seed resulted in 100 % mortality (Table 1). In fact, when rats were offered *P. hillebrandii* fruit and seed, they had consumed ~97 % of the seed tissue within 24 h, at which point the trial was discontinued. The distinction between the 24 h *P. hillebrandii* trial and the 48 h *P. maideniana* trial may provide an explanation for the appearance of a greater amount of fruit mass consumed for *P. maideniana* (Table 1).

Very little (<5 % on average) of the aboveground seedling tissue was consumed by *R. rattus* in the captive-feeding trials, and there was no significant difference between plant species for average percentage of seedling damage (d.f. = 18; $t = 0.2$; $P = 0.838$; Table 2). However, it was common for rats to tip over the pots and uproot seedlings and displace soil; they would then occupy the inside of the empty pot. It was also common for the rats to clip leaves and stack them on the cage bottom and apparently use them for bedding.

Discussion

We examined contemporary impacts of vertebrates on *Pritchardia* palms to determine seed and seedling vulnerability to predation. Both *P. maideniana* and *P. hillebrandii* experience rapid removal of fruits and seeds from the floor of a wet forest in Hawai'i, and the vertebrate responsible for such removal and likely seed destruction (based on motion-sensing camera photos and captive-feeding trials) is the rat (*Rattus* spp., probably *R. rattus*). Therefore, these findings support the hypothesis put forward by palaeoecological evidence implicating rats as a significant factor responsible for the demise of *Pritchardia* forests in Hawai'i (Athens *et al.* 2002; Hunt 2007). A further finding of our study that is perhaps less amenable to testing by palaeoecological evidence is that *Pritchardia*

Table 1. Summary of *Rattus rattus* feeding trials involving fruit and seed of *Pritchardia*. Fruits of each of the two species of *Pritchardia* were individually offered to seven rats (three fruits [~7.5 g] per individual for *P. hillebrandii* and two fruits [~12 g] per individual for *P. maideniana*) for 48 h. The percentage of fruit mass and seed mass remaining was estimated visually; seed survival was based on the presence of an intact embryo or >50 % seed mass remaining. *All seeds were destroyed (i.e. zero survivors) after 24 h for *P. hillebrandii*.

Species	Range of fruit remaining (%)	Mean ± SE fruit remaining (%)	Range of seed remaining (%)	Mean ± SE seed remaining (%)	Mean ± SE seed survival (%)
*P. hillebrandii**	88–100	96.1 ± 2.0	0–15	3.0 ± 2.1	0.0 ± 0.0
P. maideniana	0–45	24.3 ± 7.5	0–4	0.7 ± 0.6	0.0 ± 0.0

Table 2. Summary of *Rattus rattus* feeding trials involving seedlings of *Pritchardia*. A seedling (~1.9 g above-ground tissue) of each of the two species of *Pritchardia* were individually offered to each of the 10 rats for 24 h. The percentage of seedling mass remaining and damaged was estimated visually.

Species	Range of mass remaining (%)	Mean ± SE mass remaining (%)	Range of damage (%)	Mean ± SE of damage (%)
P. hillebrandii	65–100	95.5 ± 3.4	0–95	58.0 ± 13.7
P. maideniana	65–100	96.5 ± 3.5	0–90	62.0 ± 13.6

is most vulnerable to rats at the seed stage, because seedlings did not suffer damage or mortality from rats or other common vertebrates in the field. Such findings also have direct implications for the conservation and restoration of *Pritchardia* in Hawai'i, by suggesting that restoration will best be achieved by preventing seed predation or by outplanting seedlings.

Post-dispersal fruit removal (and seed predation) of *P. maideniana* and *P. hillebrandii* occurs rapidly, and few (12.5 %) available fruits/seeds escape removal by animals before germination. The high fruit and seed removal rate (>50 % after 6 days; >80 % after 42 days) in this study is similar to past rodent studies in the tropics. In a seed removal experiment conducted in Los Tuxtlas, Mexico, 60–68 % of seeds of four common species were removed after 5 days, and further study revealed that small rodents were the main post-dispersal removal agents (Sánchez-Cordero and Martínez-Gallardo 1998). In Barro Colorado Island, Forget (1992) found that 85.5 % of *Gustavia superba* seeds were removed by animals in 28 days, which included 3.8 % gnawed by rodents and 47.5 % buried by agoutis. Studying a common tropical tree, Wenny (2000) found that 50 % of the total seeds destroyed (99.7 %) were attributable to rodents. In a study excluding ungulates in a dry forest in Hawai'i, Cabin *et al.* (2000) observed the seed crop and recruitment of many native species suffered from rodent predation. On Lord Howe Island in the South Pacific, fruit and seed removal from two native palms by *R. rattus* ranged from 54 % (*Hedyscepe canterburyana*) to 94 % (*Lepidorrhachis mooreana*) (Auld *et al.* 2010). Following captive-feeding trials in New Zealand, Daniel (1973) reported that *R. rattus* consumed fruit and destroyed the two offered seeds of the native New Zealand palm (*Rhopalostylis sapida*). Seed removal rates by rodents also depend on the plant species examined, and Forget (1996) found species removal of seeds ranged from 25 to 95 %, whereas Hulme (1997) found 5–87 % removal among species. This pattern of a wide range of seed removal rates of native species was also documented with invasive rodents on Maui (0–100 % seed removal for four species; Chimera and Drake 2011) and O'ahu (15–85 % seed removal for eight species; Shiels and Drake 2011). Documentation of the negative effects of invasive *Rattus* spp. on native seeds has also occurred on many other islands (Meyer and Butaud 2009; Traveset *et al.* 2009; Wegmann 2009; Grant-Hoffman *et al.* 2010). Not only is a large range of fruits and seeds removed from the forest floor by animals, but also rodents are pervasive and are commonly responsible for such rapid removal rates.

Pritchardia seed removal by animals is patchy in space and time; seed in some locations was removed in hours or days, whereas in others it persisted for 42 days or more. The cause of the patchy seed removal remains unexplained, yet many factors can influence vertebrate foraging behaviour, including the density of vegetation cover, densities of conspecifics or other predators and available food supply. Several studies show seed predators prefer specific habitats. For example, in Los Tuxtlas, Mexico, rodent seed predators were less likely to visit and remove seeds from gaps than from primary and secondary forest (Sánchez-Cordero and Martínez-Gallardo 1998). In temperate regions, rodents completely avoided seeds in the open and foraged only under trees and shrubs (Hulme 1997). In our study, understory ground cover was variable (0–84 %), and this may have partially

contributed to microhabitats differing in likelihood of seed remaining at the end of the study.

A critical component for predicting the positive and negative effects of seed removal is the ability to determine whether removed seeds are deposited in a condition that enables them to germinate (Forget *et al*. 2004). In this study, evidence from field and captive-feeding trials suggest that rats are destroying the seeds of *Pritchardia*. On rare occasions in which seeds are not destroyed, then the distance that seed was moved in this study (>8 m), as well as the microhabitat that the seed was deposited in, can have direct effects on the spatial distribution of plant regeneration. Vander Wall *et al*. (2005) studied seed movements by rodents in the high desert of Nevada and found that rodents carried seeds 2.5 ± 3.2 m (maximum 12 m) before caching them about 1 cm beneath the soil surface. Rats in Hawai'i are not known to cache seeds (Shiels and Drake 2011), but rat husking stations (i.e. food processing stations) are commonly observed in Hawai'i (Shiels and Drake 2011) and other Pacific islands (McConkey *et al*. 2003; Wegmann 2009). Therefore, although invasive *Rattus* commonly move seeds, seed storage is unlikely. The potential for animal-mediated seed dispersal of *Pritchardia* remains unlikely given evidence from this study and that of Pérez *et al*. (2008), which found that *R. rattus* rarely leaves viable seeds of *P. hillebrandii* and *P. kaalae* during captive-feeding trials. Although the fate of the diaspores could not be determined in our field study, evidence from captive-feeding trials suggests that the rats removing the seeds are most likely consuming and destroying them (e.g. 100 % mortality for both species).

Despite non-native vertebrates being present and foraging on the ground at the study site, it does not appear that vertebrates affect the seedling stage of these two species of *Pritchardia*. Motion-sensing cameras photographed pigs and rats in the vicinity of, and passing by, the seedlings. Perhaps in more arid environments, additional non-native vertebrates such as goats may threaten *Pritchardia* seedlings (Chapin *et al*. 2004; Mosher *et al*. 2007). It is more common for invasive *Rattus* to consume seeds rather than seedlings (Grant-Hoffman and Barboza 2010; Shiels *et al*. 2013, 2014). However, on subantarctic Macquarie Island, Shaw *et al*. (2005) demonstrated that *R. rattus* reduced initial seedling establishment and seedling survival of the megaherb *Pleurophyllum hookeri*. On Palmyra Atoll, tropical Pacific, Wegmann (2009) used motion-cameras to determine that *R. rattus* caused 57–100 % of seedling mortality for three native plant species (*Terminalia catappa*, *Tournefortia argentea* and *Cordia subcordata*) during a 27-day period. One explanation for the relatively high seedling herbivory by *R. rattus* on Macquarie Island and Palmyra Atoll may be a result of few alternative food resources because of seasonality (Macquarie; Shaw *et al*. 2005) or high competition with land crabs (Palmyra; Wegmann 2009). Protecting fruit and seed from invasive rats, as well as collecting, growing and outplanting *Pritchardia* seedlings may therefore be necessary conservation measures to sustain and expand remnant *Pritchardia* stands in the Hawaiian Islands.

Conclusions

Rat foraging on the forest floor of Hawai'i wet forest (Lyon Arboretum) is pervasive. The rapid removal of *P. maideniana* and *P. hillebrandii* fruit and seed is evidence that rats forage in a range of forest-floor habitats at high frequencies, and are capable of moving relatively large fruits at least 8 m from where they were encountered. Despite fruit freshness declining from environmental exposure, most fruits that were more than a week old were still found and moved by animals. Because *Pritchardia* seeds take several months to germinate (average of 3 months for *P. maideniana* enclosed in the fruit), the fruits/seeds on the forest floor are much more vulnerable to rat predation than species that germinate quickly. The evidence from this study reveals that rats can remove, and probably destroy, high abundances of *Pritchardia* seeds rapidly from the forest floor. These findings support the notion that invasive rats could have facilitated widespread transformation of native plant communities within a few hundred years. The findings of this study suggest that better understanding of rat foraging behaviour, fruit and seed handling, as well as seed fate of both common and rare species is needed to better assess the impacts of these seed foragers on insular plant community structure.

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Contributions by the Authors

Both authors contributed to the project conception, experimental design and writing of the manuscript. A.B.S. also collected and analysed field and lab data.

Conflict of Interest Statement

None declared.

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